Contribution to the comparative histology of pulvini and the resulting photeolic movements.[1]

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WITH PLATE XXXIV.

Since the work that I have already completed upon the comparative histology of pulvini and the resulting photeolic movements is too extended to permit of presentation in these pages, the large mass of details in connection with each species will be passed over, and only an outline of the work carried out will be here attempted. The complete paper will be published elsewhere later.

Aim of study.

Inasmuch as the majority of investigators have busied themselves with seeking an explanation of the movement of leaves with motor organs without paying very great attention to their histology, the literature dealing with the structure of the pulvinus is comparatively scanty. The present work was undertaken as a contribution to the comparative histology of motor organs, hoping that a better knowledge of their structure might aid in understanding their physiology.

The work that I have already done seems to indicate that the presence of motor organs is much more general than was at first supposed. Not only the material collected, but observations in connection with the field work confirm this opinion. It remains for further study to reveal to what extent the supposition is correct.

In connection with the anatomy of the organs I have sought to give a general idea of the positions which the leaves assume at night. It was not considered necessary to measure the exact angles which the petioles form with the axes nor the angles of the leaflets with the rachis in the diurnal and

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[1]Abstract of a thesis for the degree B. S. in Botany, University of Wisconsin, June, 1894.

nocturnal positions, since the angles vary with different individuals, and with the same individual at different times. All that was sought was the general extent and direction of the movements.

I pass over the account of earlier investigations which forms the historical introduction to my paper and set forth the

Present state of knowledge as to the physiology of the motor organs.

Pfeffer[2] found that the rise of the leaves of Phaseolus, when assuming the night position, was brought about by the increase of the turgidity of the cells of the lower half of the pulvinus and a diminution of the turgor of the cells in the upper half; the reverse occurs when assuming the day position. From this it is evident that changes of an opposite nature take place simultaneously in the cells of the two opposed halves of the pulvinus.

There are three ways in which the change of the hydrostatic pressure might occur: (1) by a change in the osmotically active substances of the cell sap; (2) by a change in the elasticity of the cell-walls; (3) by a change in the resistance of the protoplasm to the escape of cell sap. The first two are shown by Vines[3] to be out of the question, and the third remains as the explanation of the changes in turgidity. With illumination comes the restoration of the protoplasm to its original condition, and the absorption of water into the cell. The change in the protoplasm being entirely invisible, it may be inferred that there occurs a rearrangement of the molecular structure or possibly the breaking down of the protoplasmic molecule. In the latter case the restoration of the original condition would simply be the building up of the protoplasmic molecule. Briefly, the mechanism of the movement may be stated as variations in the degree of turgidity of the opposed halves of the motor organs, in accordance with changes in the molecular structure of the protoplasm. The molecular changes are brought about under the influence of the alternation of light and darkness.

In connection with this subject I must mention the work of Haberlandt[4] on the conduction of "stimuli" in Mimosa

[2] Pfeffer; Die periodischen Bewegungen der Blattorgane 166. 1875.
[3] Vines; Physiology of Plants 62-64. 1886.
[4] Haberlandt; Das reizleitende Gewebe-system der Sinnpflanze. 1890.

pudica. His investigations contradict those of Dutrochet[5] and others. He finds that the impulse normally travels inside the collenchyma ring but outside the xylem of the bundles, in other words, in the phloem. When a stem is cut, drops come from special cells in the phloem and not from the xylem as was formerly supposed. The phloem of Mimosa, like that of many of the leguminous plants, is characterized by rows of somewhat larger cells than the true sieve-cells, which from the nature of their contents are known as tannin cells. He concludes that the impulse is transmitted by these rows of glucoside cells, and that in a purely mechanical manner. This is against the theory of Vines[6] that the impulse travels by the continuity of the living protoplasm, for Haberlandt found that the impulse could be transmitted through parts that had been killed by steam.

A few words in regard to what Vines terms[7] the transmission of the "stimulus." In accordance with animal physiology the use of the term is incorrect. It is not the stimulus that is transmitted but the stimulus upsets the equilibrium and the resulting impulse is transmitted. Heat as heat is not transmitted, a mechanical force as such is not transmitted, but each gives rise to impulses that are transmitted. Why then in the case of plants like Mimosa is it not the impulse from the stimulation which sets off the cells of the succeeding motor organs and causes the leaflets to fold together? We should speak of the transmission of impulses and not stimuli and in one more way unify the two sciences.

In order that we may obtain a correct idea of the movements to be dealt with, a short outline of the movements of plant organs is here given. Passing by the movements of growing organs, or auxotonic movements, which do not specially concern us, there are the movements of mature organs, or allasotonic movements, which comprise the following :

1. Spontaneous movements, resulting from conditions which we are unable to interpret.

2. Induced movements, or those resulting from stimulation. According to the nature of the stimulus we distinguish those due

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5 Vines; Physiology of Plants 583. 1886.
6 Vines; *op. cit.* 584–587.
7 Vines; *op. cit.* 582.

a. To variation in the intensity of light. Called "sleep movements;" "nyctitropic movements;" "variation movements." (Pfeffer.)

b. To variations in temperature.

c. To mechanical stimuli.

d. To electrical stimuli.

e. To chemical stimuli.

f. To intensity and direction of light, or para- and diaheliotropism.

Suggestions on terminology.

The phrase "sleep of plants" is, of course, entirely fanciful. Even as far back as the time of Senebier it was known that this Linnean phrase was not scientifically correct, yet it has continued in quite frequent use even up to the present time. The movements have also been called nyctitropic movements, among which Darwin includes the nutation movements of growing leaves. Even if we confine this term to the movements of plants with motor organs, the term is still not a good one. Etymologically it means night-turning movements; now from the nature of the movements, it is evident that since the leaves assume a different position at the approach of day, it would be just as proper to use a term meaning day-turning movements. For this reason it seems to me that some other term would be better. Since we know the real cause of the movements, the gradual variation in the intensity of the light, would not a word expressing that be better? For this reason I propose the term photeolic movements, from the Greek φως meaning light, and αιολος, variable. This term would be only applicable to movements of leaves which have special motor organs, and not to those similar movements which are auxotonic.

One more point in regard to the terminology, for it seems to me to be of importance that we use terms that are scientifically correct. The special organ of motion is commonly called, "the motile organ," or the "pulvinus," which is the same as the "Gelenkpolstern" of the Germans. In his paper on "The mechanism of movement in Cucurbita, Vitis and Robinia," Penhallow[8] speaks of tendrils as motile organs. We can not deny him the right to use this term, for tendrils certainly are motile organs. Here then is a confusion of a com-

[8] Penhallow; Mechanism of movement in Cucurbita, Vitis and Robinia. 49. 1886.

mon term, using the same for two very different structures. Burdon-Sanderson[9] speaks of the organs as "motor organs." I do not know whether it was a mere accident on his part or a premeditated change, but as he states no reason for so doing, I judge that it was the former. It is, however, a happy suggestion and therefore instead of the term which is in such common use, motile organ, I propose to adopt the term motor organ for those structures whose curvatures set in motion other passive parts. In electro-mechanics it is the motor that drives the machinery. Now the motor organ, like the electric motor, causes other structures to move, the leaf being passive and taking whatever position is necessitated by the curvatures of the motor organ. This, then, seems to me to be an especially good term, and in adopting it we shall avoid confusion in the minds of those who do not command a view of the whole subject.

Method and material.

The material for the work on this subject was collected during the summer of 1893, in the months of June, July and August. At the same time that the collection of material was made the positions of the leaves were noted. A small case containing bottles of Flemming's fluid was carried into the field; the specimens of motor organs were snipped off with a pair of scissors, leaving only such additional parts of leaves, petioles and axes as were necessary for examination, and placed immediately in the fixing fluid. The plants were visited during the day, the position of the leaflets noted, and material collected. They were again visited about dark, and specimens of the organs in their nocturnal position were obtained; at the same time a record of the position of the leaflets was made. Some leaves were slow in assuming their nocturnal position, and in those cases it was necessary to visit them later in the evening. In thus taking the observations from field specimens, I avoided the danger of vitiated observations which are possible in studying a plant out of its natural habitat. On the other hand the observations required considerable time and trouble because some of the species were local, and it was necessary to go to a distance in order to obtain specimens from them.

The specimens of the motor organs, which were placed in Flemming's fluid as soon as removed, were allowed to remain

[9] Burdon-Sanderson; The Excitability of Plants. Nature. **26:** 353, 483. 1882.

for twelve to twenty-four hours, or until they were perfectly fixed. They were then removed, washed with water, and carried through the different grades of alcohol up to 70%, where they were allowed to rest. Sections were cut and stained with either borax-carmine or hæmatoxylin, washed, then passed through 95% and 100% alcohol, cleared in oil of origanum, and mounted in balsam. For the study it was necessary to have transverse sections of the motor organ, of the petiole above and below the motor organ, and of the rachis; also median longitudinal dorsiventral sections of the organs in their diurnal and in their nocturnal positions. Over one hundred and fifty slides were prepared for the work. The borax-carmine stain was used for the majority, and it was found necessary to leave the specimens in the stain for about twelve hours, on account of the slowness with which they took it up.

Species studied.

Twenty-five species representing four families and seventeen genera were studied. The following is the list:

I. LEGUMINOSÆ.

Baptisia leucophaea Nutt., *B. leucantha* Torr. & Gray, *Trifolium pratense* L., *T. hybridum* L., *T. repens* L., *T. procumbens* L., *Melilotus alba* Lam., *Medicago lupulina* L., *Amorpha canescens* Nutt., *Petalostemon violaceus* Michx., *P. candidus* Michx., *Desmodium acuminatum* DC., *D. canescens* DC., *D. Canadense* DC., *Lespedeza capitata* Michx., *Vicia sativa* L., *Lathyrus ochroleucus* Hook., *L. venosus* Muhl., *L. palustris* L., *Apios tuberosa* Moench, *Amphicarpæa monoica* Nutt., *Gleditschia triacanthos* L.

II. GERANIACEÆ.

Oxalis corniculata L., var. *stricta* Sav.

III. POLYGALACEÆ.

Polygala verticillata L.

IV. MALVACEÆ.

Abutilon Avicennæ Gærtn.

Definitions.

In the descriptions which follow I have called the motor organ located at the base of the petiole the *primary organ.* In the pinnate leaves the whole of the secondary petiole or

petiolule is transformed into a motor organ, this I term the *secondary organ.* (Contrast with Penhallow's paper.) In the case of bi-pinnate leaves, the petiolules of the secondary leaflets may be transformed into motor organs and these I term *tertiary organs.* The term *ventral* has been used to indicate the upper side of the organ, leaf-blade or petiole, that is, the side toward the axis in the bud, the *dorsal* being the lower side or that which is away from the axis in the bud. Following the example of Penhallow[10], I have used the term hypodermal tissue to mean the tissue between the stele and the epidermis which is derived from the periblem. Vines[11] calls this *extra-stelar* fundamental tissue. In the motor organ the pith is either pushed to one side and the cell-walls become thickened or it remains in the center of the stele; when the former is the case, the stele is generally somewhat kidney shaped in cross section, the remnant of pith occupying the depression. This depression I have termed the *hilum of the stele* in order to facilitate description. In the descriptions I have given the external appearance of the motor organs and the changes in position of leaves from normal diurnal positions to the nocturnal positions. I have then in each case given the anatomy of the organs, beginning with the primary and following this with the secondary and the tertiary organs when present.

From the twenty-five species described I select one, which though treated at greater length than the majority is best adapted for illustration.

Melilotus alba.

Melilotus alba shows well developed motor organs and consequently very marked movements. It has a primary motor organ which will be noticed as a slight thickening of the petiole just above the bract-like stipules, each of which contains a well developed schizostele. These schizosteles arise half way around the central stele of the axis and pass upwards and towards the base of the pulvinus, where just before uniting with the middle schizostele, they are almost at right angles to the axis. These three schizosteles of which the center one is the largest unite in the center as they pass through the motor organ proper. Besides being an enlarge-

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[10] Penhallow; *loc. cit.* 76.
[11] Vines; Students' Text Book of Botany 146. 1894.

ment of the petiole the organ is noticeable on account of its darker green color. The secondary motor organ, as in Trifolium, constitutes the whole of the petiolule, but here there is a rachis intervening between the mesopodium and the pulvinus of the terminal leaflet. [This was referred to when speaking of Trifolium procumbens in the preceding genus.] Unlike those of Trifolium, the organs do not show any difference in size as they are continued on into the mid-rib, but shade off gradually so that their limit can only be determined externally by their difference in color. The rachis continues for about half an inch before the terminal leaflet is given off and the organ of this leaflet is a little smaller than the rachis, there being quite an abrupt change in size, as shown in plate XXXIV, figs. 1 and 2.

In the normal diurnal position the petiole forms a right angle with the internode above its insertion, and the three leaflets are spread out in a horizontal position. The leaf shows other very marked movements not photeolic, and one of these may be noted early in the morning when the sun is still in the east. The petiole curves so as to bring the plane of the laminæ at right angles to the incident rays of the sun. If the plants are visited in the late afternoon it will be found that the upper surfaces of the leaflets are similarly turned towards the setting sun. This is due to the so-called transverse heliotropism and is to be separated from the movements brought about by the variation in the intensity of light. If the plants are observed in the hottest part of the day they will be found to have assumed a position different from the one just described. The blades of the leaves are brought to occupy a position parallel to the incident rays of the sun, by turning upwards; this movement is connected with the protection of the chlorophyll from the intense rays of the sun, and is due to the so-called paraheliotropism. These movements are mentioned so that it may be understood that they are not similar to, and have not been confused with, the phottteolic movements.

In assuming the nocturnal position the primary petiole approaches the axis above its insertion, passing through an angle of 20–30°, thus coming to make an acute angle with the axis. The two lateral leaflets turn upwards so as to bring the upper faces together, but they never twist upon their axes. The terminal leaflet approaches the axis, sometimes

directly without any twisting, while at other times a slight twist is made. They thus assume nearly the same position as the leaflets of T. repens, only the position seems different on account of the upright growth of the axis.

Darwin[1][2] describes the "sleep movements" of a large number of species of the genus Melilotus, and as the type of their movements, he selects a case altogether different, in that the movement is the exact reverse of what I have found in Melilotus alba, although this is one of the species that he enumerates. Special pains was taken to make sure of this movement and plants were visited again and again with always the same result. It could hardly be that Darwin made a mistake and as he mentions a similar movement in one species at a different time, it is possible that the movement may sometimes differ in the same species. From this reversion of the movement to the Trifolium type, Darwin is inclined to speculate, and regards it as an indication of the close relation of the two genera. Since all photeolic movements are either up or down I can see no basis for such speculation.

Primary organ.—The pulvinus of the petiole as seen in the cross section is kidney shaped, fig. 4, the hilum being directed upwards or towards the ventral side of the petiole. The dorsiventral diameter is about 1.4^{mm}, the lateral diameter 1.75^{mm}, while the length is only about 1.4^{mm}. From these measurements it will be seen that the organ is quite short being only as long as its dorsiventral diameter. In the diurnal position the organ has a single transverse depression on each side, that on the ventral side being somewhat closed up, but not as deep as the one upon the dorsal side. In the nocturnal position there is a marked change in the outline; the transverse depression on the dorsal side becomes less marked as the petiole approaches the axis, while the motor organ, on its ventral side, is thrown into transverse folds for its entire length, (3 or 4 folds) the depth of the depressions depending upon the degree of movement that has taken place. As a general rule the depressions are deeper at the base of the organ and become more shallow towards the distal end.

There is a gradual change in the epidermis in passing from the leaf or petiole, so gradual indeed that it is impossible to tell exactly where the cells belong to the one or the other region. The epidermal cells of the pulvinus are of about

[1][2] Darwin: Movement of Plants. 346, *fig. 140.* 1880.

equal dimensions radially and tangentially, but are shorter in the longitudinal direction in accordance with the general type of motor organ cells. In consequence of the thickening of the walls the cell cavities are more or less spherical, fig. 3. The epidermal cells of the dorsal side are larger than those on the ventral side. The internal walls are much thicker in the longitudinal direction than the external walls, and very much thicker than the radial walls (fig. 3). The external wall also shows longitudinal ridges as in Trifolium pratense and other species.

The cells of the hypodermal tissue are different upon the upper and under sides of the organ. Those immediately beneath the epidermis are of about the same size as the epidermal cells, but towards the center the first few cells increase in size, then there is a decrease until the central stele is reached where they are even smaller than the epidermal cells. The cells of the dorsal side of the motor organ in the region of the hilum are smaller than those of the other side and their walls are more uniformally thickened while the cell cavities are generally four sided in cross section. The remainder of the hypodermal cells are of the collenchyma type, fig 3. They are very much thickened at the corners and the middle lamellæ are very marked. The side walls, although they look thin when compared with the thickened corners, are yet very much thicker than the walls of the adjacent parenchyma. Upon the ventral side of the organ in the region of the depression, which remains permanent, the cell walls are very thick and the cells irregular in shape. In some cases the opposite walls nearly touch each other, and when the nocturnal position is assumed the cells in the region of all the transverse depressions become very much distorted in shape. In the region of the central stele there are a few intercellular spaces, but towards the periphery they are entirely absent. The cells near the axis cylinder contain an abundance of chlorophyll, but those near the surface have a less abundant supply. Like all those previously described the cells have a peripheral layer of protoplasm, with the center occupied by a large vacuole.

Cross sections of the hypopodium were cut, and the origin of the bundles from the axis which was externally indicated, was confirmed. The purely mechanical advantage of this arrangement is at once clearly seen, and when it is noted that these three schizosteles come together at the base of the pul-

vinus and pass through that organ as a single cylinder, separating again as soon as beyond the limits of the motor organ, one is again impressed by the mechanical advantage which is gained by this course. As shown in the cross section the central meristele is kidney shaped in agreement with the form of the organ and is entirely surrounded by a cylinder of bast fibers. (The outline is shown in fig. 4.) The cells with the thickened walls at the hilum, which are considered to represent the remnant of the pith, have very much thicker walls than the remainder of the bast fiber layer which is made up of the bast fibers belonging to the phloem of the bundles. As seen in the longitudinal section the cells at the hilum are found to be short fusiform cells, while the latter are much longer and contain straight cross partitions which are much thinner than the longitudinal walls. The phloem forms a continuous ring around the xylem except at the hilum. The xylem vessels, spiral, pitted and reticulated, radiate from the hilum and between them are well marked pith rays the cells of which are filled with granular protoplasmic contents. From the short longitudinal dimensions of the cells of the motor organ proper, it might be thought that on account of the tensions set up, the cells of the vascular bundles would likewise be shorter than elsewhere. This supposition is confirmed by observation. The pitted and spiral vessels show cross walls much more frequently than in the general bundles of the plant.

Secondary organ.—The secondary pulvinus is nearly circular in cross section, 0.7^{mm} in diameter. The length is 1.4^{mm}, i. e., twice as great as its diameter. As seen in the cross section the epidermal cells are of the same size as the hypodermal collenchyma cells but their longitudinal dimensions are less than the same of the collenchyma. The external epidermal wall is very thin and covered with a thin cuticle which shows longitudinal ridges as already described for the primary motor organ. The radial diameter of the cells is about twice their longitudinal dimension, but beyond the limits of the organ their three dimensions are about equal, or if any difference is to be detected the longitudinal is greater.

The whole of the hypodermal cells from the epidermis to the vascular cylinder show a marked regularity in size and form; they are arranged in regular longitudinal rows, but do not fit together in the manner of all those previously des-

cribed but have square end walls. They are of the same collenchyma type as shown in the organ of the petiole, but the thickening at the corners is not quite as marked. In Trifolium repens the walls of the pulvinus parenchyma cells are slightly thicker than the walls of the adjacent parenchyma. A few of the cells for that organ are shown in fig. 5; as compared with those, a few cells from the organ of Melilotus alba are shown in fig. 6. The difference in the thickness of the cell walls is to be noted. The cells are about equal in their tangential and radial dimensions but their length is slightly less. No intercellular spaces whatever could be detected, but the whole of the hypodermal cells are richly filled with chlorophyll bodies, while the protoplasm always occupies the periphery with a large vacuole in the center.

In the diurnal position the organ is slightly curved and shows very marked and regular transverse wrinkles for the entire length. When the organ assumes its night position it becomes more curved; the wrinkles on the ventral side become more marked while those on the other side are to a certain extent obliterated, figs. 7 and 8. These organs are contractions rather than enlargements of the petiolule. The same distortion of the cells in the region of the transverse depressions is to be noted as in the primary organ.

The schizosteles, as they emerge from the primary organ, traverse the petiole in the position shown in fig. 9 and give off lateral branches to the secondary motor organs in which they still occupy the center. The stele with its surrounding bast fibers is circular in cross section to agree with the form of the organ itself and it shows the same remnant of pith as in previous cases. By comparing the cross sections of the steles of the petiole and motor organs, it is found that the elements have been reduced in size; the bast fibers have thicker walls and are decidedly smaller, while the sieve cells have undergone such a modification in the thickness of their walls that it is almost impossible to tell which are bast fibers and which sieve cells, so closely do the two regions merge into each other. Otherwise the arrangement is very similar to that described for the primary organ, so no further description is needed. In the rachis the schizosteles occupy the same position as in the petiole and at the end come together to form the central stele of the terminal leaflet.

Conclusion.

From the study of the twenty-five species, I have found that there are, considering their diversity, many striking resemblances in the external and internal anatomy of the motor organs, of which I here give a short summary:

1. Organs may be found at the base of the petiole, and as such they are termed primary organs. In the species considered the primary organ may be altogether absent or represented by an imperfect development. As a general rule simple leaves do not possess pulvini; but one exception has been noted in the case of Abutilon Avicennæ, in which the organ is at the base of the leaf blade, or epipodium. This, however, I consider as a primary organ. The petiolules of each leaflet of pinnate and bi-pinnate leaves are transformed into motor organs, the secondary and tertiary organs. In the case of pinnate leaves, whenever any pulvini are present, it is always these which are found, no examples being discovered in which a primary organ was present without secondary organs.

2. The organs generally show a difference in color from the adjacent tissue. In the organs containing chlorophyll the color is darker green, which it must be concluded is due to the fact that the organ contains but few intercellular spaces. The pulvini which do not contain chlorophyll are generally yellowish. This color is due to the presence of yellow coloring matter, probably xanthophyll. In all the color may be modified by trichomes, and in Abutilon Avicennæ there is a red coloring matter in the epidermal cells.

3. As might be expected, different stages in the development of the pulvini are found in the species described. All gradations, from the very simplest indication to the perfectly developed organ, are to be found. These rudimentary pulvini are always at the base of the petiole and never secondary or tertiary organs The beginning development is to be detected by the enlargement of the base of the petiole, the modification of the hypodermal cells to agree with the motor organ type, and in the convergence of the schizosteles towards the center to form a single cylinder.

4. The organs have a variety of forms in cross section. The organs of the petiole, the primary organs, are more generally kidney-shaped although they may be circular or oval. The secondary pulvini are more commonly circular or oval in cross section, but different forms occur, varying from flattened

heart shape to almost triangular. In organs which are not circular, the lateral diameter is generally the greater although the exact reverse is the case in a few species. In the majority of organs the length is generally about twice the diameter; a few however were found in which the diameter was equal to the length.

5. The epidermis is fairly well developed when compared with the adjacent epidermis, and *well* developed when compared with the remainder of the motor organ tissue. The cells are shorter in the longitudinal direction than those of the leaf or petiole and their longest diameter is generally in the radial direction. The epidermis is generally covered with trichomes but in no instance could any stomata be found within the limits of the motor organ. The hypodermal cells are always smaller than the parenchyma cells of neighboring parts. They are always very short in the longitudinal direction, while the radial and tangential dimensions are sometimes equal to each other, but as a general rule the radial dimension is the greater. The cell walls are generally thicker than the walls of the adjacent parenchyma cells, and the protoplasm always occupies the periphery of the cells. The cells may be arranged in quite regular longitudinal rows, or on the other hand the arrangement may be quite irregular. The hypodermal tissue is to be regarded homologous with the mesophyll of the leaf. There are three types of hypodermal cells: (*a*), the parenchyma type; (*b*), the collenchyma type, or those which show thickened corners in the cross section; (*c*), a type intermediate, in which the cells have walls that are uniformly thickened.

6. Very few intercellular spaces could be detected and these only near the central stele; they are very small when compared with the intercellular spaces of adjacent parts.

7. The completely developed organ is always traversed by a stele which is entire and completely surrounded by a layer of non-lignified bast fibers. The meristele, in those leaves with primary organs, arises from the axis as three separate strands; these fuse to form the meristele of the organ and so close is the union that it is impossible to make out these three in the cross section. The same may be said of the stele of the secondary organ which is simply a branch of the meristele of the petiole. The stele may be central, or pushed to one side, in which case it is excentric. The remnant of the pith may

be in the center of the stele or it may be represented by the thickened cells at the hilum, which is always on the dorsal side of the organ. Generally speaking the elements of the steles are poorly developed.

8. The well developed organ always shows marked transverse folds even in the diurnal position, which become changed when the curvature of the organ becomes greater or less. Many organs show a compression and distortion of the cells in the region of the transverse folds.

9. Some organs must be regarded as enlargements according to the old idea while others are distinctly contractions. The former is generally the case with primary organs and the latter more commonly with secondary and tertiary organs.

Madison, Wis.

EXPLANATION OF PLATE XXXIV.

All figures except fig. 5 represent Melilotus alba.

Fig. 1. Diurnal position of leaf turned towards the west.
Fig. 2. Nocturnal position.
Fig. 3. Epidermal and collenchyma cells from the cross section of the primary organ.
Fig. 4. Diagram of cross section of primary organ.
Fig. 5. Trifolium repens. Hypodermal parenchyma cells from motor organ. Longitudinal section.
Fig. 6. Cells from longitudinal section of secondary organ.
Fig. 7. Diagram of longitudinal section of secondary organ, nocturnal position.
Fig. 8. The same, diurnal position.
Fig. 9. Diagram of cross section of petiole.
Fig. 10. Diagram of cross section of secondary organ.